ASPECTS OF THE FEEDING BIOLOGY AND BEHAVIOR

OF TWO PARROTFISHES (FAMILY SCARIDAE)

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ASPECTS OF THE FEEDING BIOLOGY AND BEHAVIOR OF TWO PARROTFISHES (FAMILY SCARIDAE)

A
THESIS

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ABSTRACT

Aspects of the behavior and feeding biology of two parrotfishes, *Scarus jonesi* (Streets) and *S. gibbus* Ruppell, were studied at Eniwetok Atoll, Marshall Islands. A number of adaptations to maximize utilization of food resources and minimize possible physiological stress from ingestion of large amounts of calcium carbonate were examined. Although gut pH of *S. jonesi* was on the alkaline side of values reported for rays and teleosts, calcium carbonate was inferred to dissolve within pH and time constraints of parrotfish digestion. Observations suggest that acidification of gut contents results from the introduction of slightly acidic bile and possibly from the acidic protoplasm from triturated algal cells.

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I have a particular debt to Mr. Rhett McNair of Honolulu, Hawaii. Rhett was not only a warm friend and patient teacher, but he constructed for me an awesomely powerful powerhead of his own design. Thus I was able to instantly stop an aggressive shark less than eighteen inches away, killing him with a single shot.

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TABLE OF CONTENTS

ILLUSTRATIONS

INTRODUCTION

The parrotfishes (Family Scaridae) are commonly the most abundant fishes of moderate size on a coral reef, and occur in all marine habitats associated with the reef (Harry, 1953). There has been considerable disagreement about the feeding habits of scarids, particularly whether or not they feed on live coral polyps. It is evident, however, that the feeding habitats of parrotfishes result in the ingestion of considerable calcium carbonate in the form of scraped coral rock as well as algae. This intake of carbonate could result in metabolic, especially acid-base, problems. It appears that parrotfishes have a series of adaptations to deal with carbonate in the gut, and this study is the first part of an investigation into these adaptations.

Presumably ingestion of carbonate is adaptive but to date no one has really shown how. Uptake of carbonate sand, when scarids graze on marine grasses, may simply serve as a milling agent (Randall, 1967). Sand may also provide an additional food source, the filamentous Myxophyceae (Cyanophyta) and other minute algae that may be imbedded in the sand for protection from direct sunlight (Sargent and Austin, 1954). This may account for the observations of Longley and Hildebrand (1941) who reported two parrotfish feeding actively on what appeared to be perfectly bare coral sand. Specialized dentition may permit exploitation of endolithic algae unavailable to other grazers such as surgeonfishes (Family Acanthuridae) (Randall, 1963) or allow more effective utilization of calcareous algae. Therefore, some dissolution of carbonate in the gut could make more plant material available for digestion than could

trituration alone. Thus, dissolution of carbonate in a pH environment more acidic than sea water could be adaptive if the resultant dissolved carbonate did not stress the CO_2 transport mechanisms of the blood.

This study is a preliminary examination of some aspects of parrotfish biology relevant to feeding habits and carbonate ingestion. Included are general behavior, alimentary morphology, and aspects of scarid physiology dealing with the ingestion of calcium carbonate. I examined pH regimes throughout the scarid digestive tract, food transit times, and evidence for the dissolution of carbonate within the pH and time constraints of parrotfish digestion.

METHODS AND MATERIALS

This study was conducted at Eniwetok Atoll, Marshall Islands. Fishes were collected from Eniwetok Island north to Japtan Island.

Scarus jonesi (Streets) was abundant in the inshore lagoon habitats around Eniwetok Island, and, therefore, was chosen as the primary study species. *Scarus gibbus* Ruppell, a moderately large parrotfish occurring in lesser numbers and often within the *S. jonesi* aggregations, was also used. A total of 200 hours of observations was made by free and scuba diving. Collection was by spearing during the day and by hand netting in rocky shallows at night. Fishes were immediately returned to the laboratory in buckets of sea water and maintained in running seawater aquaria awaiting experimentation.

Gut pH samples were taken in the following manner. A fish was anaesthetized in a 0.00015 (W/V)% solution of tricaine methanesulfonate (MS-222) in sea water. The abdominal cavity was opened, and gut contents were sampled with a syringe from each of the four major regions of the alimentary canal: pyloric caecum, small intestine, large intestine, and rectum. All members of the Scaridae are stomachless. Utilization of a Radiometer micro pH meter with a Beckman microelectrode made it possible to take small (0.15 ml) samples. Blood samples were taken by cardiac puncture for comparison of blood pH with that of gut samples. All samples were obtained from live fishes exceeding 1 Kg in weight.

The t' statistic of Steel and Torrie (1960: 81) was used in comparing the means of data. For graphic comparison of means, the 95%

confidence limits were determined (see Simpson, Roe, and Lewontin, 1960:158).

GENERAL BEHAVIOR

Scarus jonesi was the most common parrotfish of the inshore lagoon habitat of Eniwetok Island (this paper) and of Japtan Reef (P. Helfrich, unpublished). Often they would form joint feeding aggregations with *S. gibbus* and sometimes the surgeonfish *Acanthurus bleekeri* Gunther (Family Acanthuridae). These scarids were predominantly found around patch reefs of the reef flat, with somewhat smaller individuals found together with young *S. forsteri* Cuvier and Valenciennes in one meter of water or less. Movement over sand flats between patch reefs was rapid and direct, giving the impression that scarids follow established routes. Several *S. gibbus* appeared solitary, and would retreat to the same home cave when approached (see Winn and Bardach, 1960, on home caves).

Numerous *S. jonesi* could be observed at night in less than one meter of water in the rocky shallows of both lagoon and seaward shores. In the shallows exposed to tidal currents no mucous envelopes were observed, and the fish were never encountered in the state of sleep so often described for parrotfishes (Winn, 1955; Starck and Davis, 1966). About thirty minutes before sunset *S. jonesi*, *S. gibbus*, and *A. bleekeri* formed large milling aggregations near lagoon patch reefs. They took shelter in crevices of the reefs from fifteen to thirty minutes after sunset. Although the surgeons remained inactive but alert, the parrotfishes were completely quiescent. This agrees with the observations of many authors that parrotfishes are strictly diurnal (e.g. Winn and Bardach, 1959, 1960; Schroeder, 1964; Hobson, 1965).

Parrotfish aggregations were observed feeding in seaward, inter-island, and island lagoon reef habitats. With rising tide, parrotfishes of the seaward and inter-island areas grazed intensively on the seaward algal flat. During low tide parrotfishes grazed intermittently in the surge channel and lagoon patch reef areas respectively. Scarids in island lagoon reef areas fed intermittently regardless of tidal stage, except along rocky shorelines where additional algae-covered substrate was made available by high tide. This latter area was intensively eploited while available.

Many hundreds of parrotfishes were observed during about 200 hours of underwater observations. During this time *S. jonesi* and *S. gibbus* were observed feeding only on dead coral and filamentous algae. Live coral was never taken. Examination of gut contents revealed only fragmented algal cells and calcium carbonate grains. No coral polyps or polyp fragments were observed.

ALIMENTARY MORPHOLOGY

Several authors have dealt with the alimentary anatomy and histology of parrotfishes (Al-Hussaini, 1945, 1947, 1949; Gohar and Latif, 1959). Figure 1a shows the viscera of *Scarus jonesi in situ* upon removal of the left abdominal wall. Extending posteriorly from the pharyngeal mill (Fig. 1b) is a short tubular esophagus which is separated from the small intestine by a pyloric valve. Posterior to the valve, a pyloric caecum extends from the small intestine; these are closely invested by the left lobe of the liver (hepatopancreas). Al-Hussaini (1945) suggests the pyloric caecum functions as a receptacle for food storage. The gall bladder (Fig. 1c) lies ventral to the anterior end of the small intestine, and empties via a duct into the dextroventral side of the pyloric caecum. The small intestine appears as a smooth tube extending to the posterior of the abdominal cavity, curving ventrally at the bladder. Here the large intestine with its many transverse folds arises, completing two loops and terminating in a relatively smooth-walled rectum.

Several authors have shown that there is a positive correlation between feeding habits of fishes and the ratio of the gut length to standard length (Suyehiro, 1941; Al-Hussaini, 1947, 1949). This ratio is called the "relative gut length." Measuring from the pyloric valve to the posterior end of the rectum, the relative gut length for *S. jonesi* averaged 2.7 with a range from 2.6 to 2.8 (n=4).

Figure 1a. The viscera of *Scarus jonesi in situ* upon removal of the left abdominal wall.

Figure 1b. The viscera *in situ* upon removal of the left lobe of the liver, the left ovary, and the left operculum.

Figure 1c. The viscera with the small intestine and part of the large intestine reflected.

KEY TO FIGURE 1

1. pharyngeal mill
2. esophagus
3. pyloric caecum
4. small intestine
5a. large intestine - first loop
5b. large intestine - second loop
6. rectum
7. gall bladder
8a. liver - left lobe
8b. liver - right lobe
9a. ovary - left
9b. ovary - right
10. gas bladder
11. urinary bladder

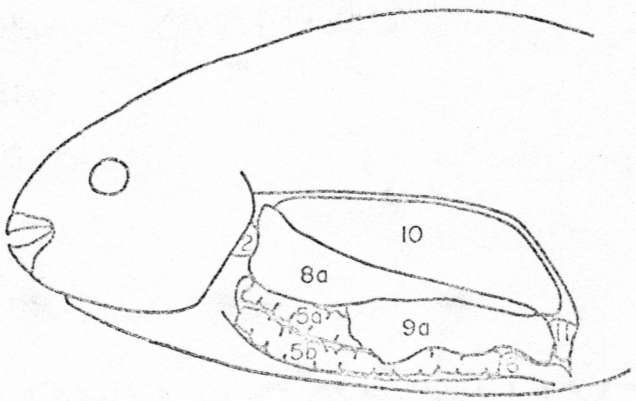

FIGURE 1a

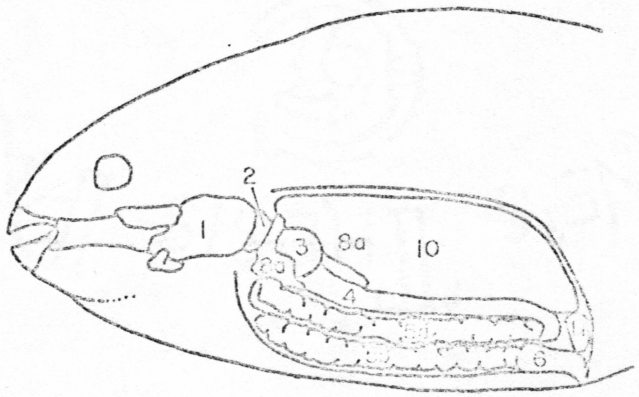

FIGURE 1b

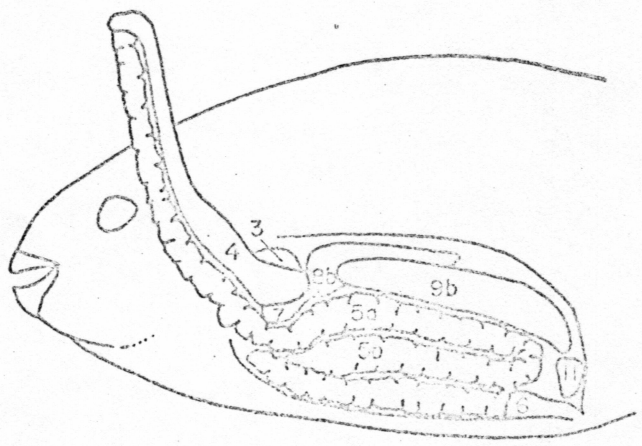

FIGURE 1c

The digestive tract of *Scarus jonesi*. For explanations of the different views and symbols, refer to the legend on the preceding page.

PHYSIOLOGY OF DIGESTION

Table 1 compares gut pH data for the three categories examined in the study: *Scarus jonesi* taken during the feeding period; *S. gibbus* taken at the same time; and *S. jonesi* taken four to six hours after termination of feeding. The feeding *S. jonesi* had a mean blood pH of 7.17 (n=4) and a mean bile pH of 6.95 (n=4). Sea water had a pH of 8.2. Figure 2 portrays the data from Table 1.

Since, in most fishes, intestine contents become increasingly alkaline posteriorly (Barrington, 1957; Langley, 1971), one tailed t' tests were used to compare all combinations of gut regions in both feeding categories. The 95% confidence interval was selected for tests of significance. The results showed that in feeding *S. jonesi*, the pH values of the pyloric caecum and small intestine are not significantly different, while all other combinations are different. In feeding *S. gibbus* the pH values of the pyloric caecum, small intestine, and large intestine are not significantly different, while the rectum is significantly more alkaline than all three. Two tailed tests were used to compare the gut regions of the two feeding groups, showing that the pH of each gut region in feeding *S. jonesi* is significantly different than that of feeding *S. gibbus*.

Coral debris from the large intestine of *S. jonesi* was placed in a tris-buffer solution (pH 6.8) similar to the pH environment of the small intestine. In two experiments individual carbonate grains were observed to dissolved perceptibly within one hour.

Table 1. Mean pH of gut samples ($\bar{y}$) for the three categories of fish tested, standard deviation (s), and sample size (n).

SAMPLE GROUP		PYLORIC CAECUM	SMALL INTESTINE	LARGE INTESTINE	RECTUM
S. jonesi (feeding)	$\bar{y}$	6.8	6.9	7.5	8.2
	s	.379	.417	.700	.560
	n	21	30	31	22
S. gibbus (feeding)	$\bar{y}$	6.4	6.5	6.4	7.5
	s	.187	.148	.198	.268
	n	4	4	4	4
S. jonesi (nonfeeding)	$\bar{y}$	7.2	7.5	7.6	—
	n	2	1	3	—

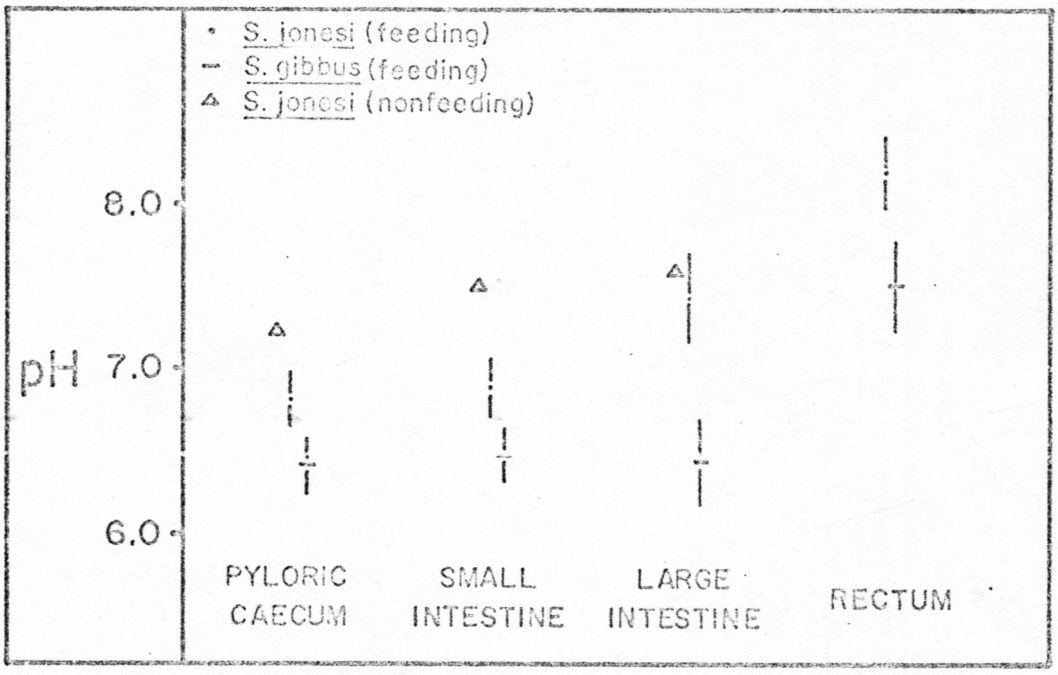

Figure 2. Mean pH of gut samples for the three categories of fish with 95% tested confidence intervals indicated by the vertical bars. No confidence intervals are given for the nonfeeding *Scarus jonesi* since the sample size was very small.

Parrotfishes were observed defecating at 1030 hr with first light at approximately 0700 hr. Speared individuals at this time showed very full digestive tracts. Fishes taken at 0100 hr with last light at approximately 1930 hr had empty tracts. Thus, considering the strictly diurnal activity of scarids, a transit time, the time from ingestion to defecation, on the order of three to five hours is suggested. This is in contrast to Bardach (1961) whose data indicate a transit time of about 12 hours in West Indies parrotfishes. Scarids taken during the feeding period often had empty stretches of digestive tract separating sections turgid with food, suggesting intermittent feeding activity.

DISCUSSION

The literature presents a confusing picture of the nature of the food consumed by parrotfishes. Some authors, such as Owen (1866) simply refer to parrotfishes as "coral feeders" not specifying if coral polyps or coral skeletal material is implied. Gerlach (1961) only mentions feeding on live coral, and suggests that parrotfishes are carnivores. Other authors report algae and coral polyps among the stomach contents and classify scarids as omnivores (Harmer and Shipley, 1932; Al-Hussaini, 1945, 1947; Gohar and Latif, 1959; Hiatt and Strasburg, 1960). Other authors consider parrotfishes as herbivores, with only incidental animal matter ingested (Jordan and Evermann, 1898; Beebe and Tee-Van, 1933; Gregory, 1933; Longley and Hildebrand, 1941; Odum and Odum, 1955; Bakus, 1967; Randall, 1967). Bardach (1959) classified juveniles as herbivores and adult parrotfishes as omnivores. Gohar and Latif (1961) concluded from a study of carbohydrases that scarids are not herbivores. Randall (pers. comm.) considers parrotfishes to be herbivorous, and suggests that feeding on live coral is probably restricted to the genus *Bulbometapon*. Randall's observations agree with my own at Eniwetok Atoll and in the Florida Keys. I have never witnessed any members of the genera *Scarus* and *Sparisoma* feeding on live coral, but rather on dead coral, strands of filamentous algae, and the sea grass *Thalassia*.

The mean relative gut length of *Scarus jonesi* is 2.7. Gohar and Latif (1959) found that carnivorous fishes had a range of relative gut lengths from 0.6 to 2.4, omnivores from 1.3 to 1.6, coral feeders (including parrotfishes) from 1.5 to 4.2, and herbivores from 3.7 to

6.0. The relative gut length of *S. jonesi* falls only within the range of "coral feeders," in which Gohar and Latif included such genera as *Scarus*, *Balistes* (Family, Balistidae), *Tetrodon* (Family, Tetraodontidae), and *Diodon* (Family, Diodontidae). The latter three groups feed on live coral polyps, and therefore ingest significant amounts of calcium carbonate in the process (Hiatt and Strasburg, 1960). These relative gut lengths suggest at least one characteristic common to live and dead coral feeders. Correlations of relative gut length with diet such as Suyehiro (1941) has made may not be meaningful unless the surface area of the intestinal mucosa (Al-Hussaini, 1949) is considered as well.

My data indicates that *Scarus jonesi* is an herbivore that ingests large amounts of calcium carbonate. Since other members of the genus Scarus have been shown to be stomachless, I infer that *S. jonesi* has no histological mechanism for production of hydrochloric acid. Accordingly, the gut pH of feeding individuals is noticeably more alkaline than the gastric pH of carnivorous fishes. The pharyngeal mill has taken over the mechanical function of the stomach, while the intestine is now solely responsible for the chemical functions (Barrington, 1957).

Although lack of HCl production may be adaptive in reducing possible acid-base stress from increased carbonate dissolution, the actual selection pressure that originally led to the loss of the stomach in scarids remains unclear. Further evidence that increased pH values in the alimentary canal are adaptive in this way may be inferred from comparisons of my data with the existing literature. MacKay (See Barrington, 1957) found that intestinal pH values of rays and teleosts with full stomachs ranged from 4.6 to 7.4. On the otherhand, the pH

regime in feeding *S. jonesi* grades from 6.8 in the pyloric caecum to 8.2 in the rectum, and thus, is on the alkaline side of the range reported for rays and teleosts.

Although scarids cannot secrete HCl into the foregut, this region in feeding individuals is more acidic than sea water (see Table 1). These data agree well with pH data on two other parrotfishes, *Scarus ghobban* and *S. harid* (Gohar and Latif, 1961). Two possible sources for this lowered pH are proposed: bile, and the cellular contents of ingested algal cells. The bile of *S. jonesi* is about 0.2 pH units more acidic than blood. A number of authors have reported slightly acidic bile in fishes (Vonk, 1927; Babkin and Bowie, 1928; Babkin, 1929; MacKay, 1929). Thus, one of the normal physiological roles of bile seems to be reversed in these fishes. Dawson (1966) reports that protoplasm in algal cells is often fairly acidic, with pH ranging from 4.0 to 6.8. It appears that a pH environment in scarids is created in the pyloric caecum and small intestine during feeding which may be sufficiently acidic to perceptibly dissolve coral rubble. This dissolution may make additional food sources available, such as bacteria, boring fungi and algae, and other organic material within dead coral skeletons (Di Salvo, 1969; Kohlmeyer, 1969).

SUMMARY

1. *Scarus jonesi* and *S. gibbus* are herbivorous.
2. The pH regime in feeding *S. jonesi* grades from 6.8 in the pyloric caecum to 8.2 in the rectum.
3. The acidic environment in the foregut is thought to result from the introduction of slightly acidic bile and possibly the acidic protoplasm from triturated algal cells.
4. One function of bile is apparently reversed in scarids. Instead of making intestinal contents more alkaline, it helps to acidify the intestinal environment.
5. Gut pH in *S. jonesi* is on the alkaline side of the range of values reported for rays and teleosts. This may be adaptive in minimizing acid-base stress resulting from dissolution of ingested carbonate.
6. Gut pH regimes differ between *S. jonesi* and *S. gibbus*.
7. Gut pH regimes may differ in *S. jonesi* according to feeding condition.
8. Calcium carbonate was observed to dissolve within the pH and time constraints of parrotfish digestion.
9. Transit time in scarids one kilogram or heavier is from three to five hours.

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THIS SUCKS